

A NEW GENUS OF BEAVER  
(MAMMALIA: CASTORIDAE: RODENTIA) FROM THE  
ARIKAREEAN (OLIGOCENE) OF MONTANA AND ITS  
BEARING ON CASTORID PHYLOGENY

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ABSTRACT

The holotypes of two Arikareean castorids from Montana, *Steneofiber complexus* Douglass and *S. hesperus* Douglass were reexamined in light of recent synonymies of these species with other European and Asian species. The two Montana species are synonyms but are not synonymous with any previously described species of castorid from either Europe or Asia. A new genus, *Neatocastor*, is named for the Montana beaver, *N. hesperus*.

The new genus is most closely related to the otherwise Chadronian to Whitneyan-aged castorid *Agnotocastor* Stirton and the Hemingfordian to Barstovian *Amblycastor* Matthew. A combination of retained primitive characters and derived characters of the skull and dentitions of these genera unite them systematically. This group of genera represents an early offshoot of the Castoridae that is not ancestral to any other group of castorids.

INTRODUCTION

Douglass (1901) described two beavers from the Miocene of Montana, *Steneofiber hesperus* and *S. complexus*, but was uncertain of their age of occurrence. Matthew (1902:301) listed these species as "White River" in age (= Oligocene). Stirton (1935) transferred both of these species to his new genus *Monosaulax* and placed them questionably in the late Miocene (= Barstovian). Most recently, Xu (1994) synonymized these two species (along with four other Eurasian species) under *Steneofiber hesperus* and recognized them as occurring in the late Arikareean. A detailed examination of the holotypes of *S. hesperus* and *S. complexus* has allowed for the recognition of a new genus of castorid and a detailed discussion of the relationships of these species.

Dental nomenclature used follows that of Stirton (1935). Abbreviations for institutions are: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; KU, University of Kansas, Museum of Natural History; USNM, National Museum of Natural History, Smithsonian Institution; YPM-PU, Princeton Collection, Yale-Peabody Museum.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Superfamily Castoroidea Gray, 1821

Family Castoridae Gray, 1821

*Neatocastor*, **new genus**

*Type and Only Species*.—*Steneofiber hesperus* Douglass, 1901.

*Range*.—Arikareean (late Oligocene) of Montana.

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*Diagnosis.*—Castorids with elongate rostra; posterior palatine foramina within palatine bone; dorsally, nasals extend more posteriorly than premaxillaries; complex occlusal pattern cheek teeth (multiple fossettes preserved on worn teeth, irregularities of enamel preserved on lophs); cheek teeth subhypsodont and rooted;  $dP^3$  present; anterior face of upper and lower incisors broadly convex anteriorly; upper cheek tooth rows parallel, widely spaced; premolars subequal in size to molars in early stages of wear.

*Etymology.*—Greek, *neatos*, last or utmost; Latin, *castor*, beaver.

*Discussion.*—The cheek tooth patterns of *Neatocastor* are more complex than in most other castorids which have a simplified series of reentrant valleys. The rostrum of *Neatocastor* is more elongated than in other castorids, similar to the elongation seen in eutypomyids. The skull and dentition of *Neatocastor* most closely resemble those of the Chadronian to Whitneyan castorid *Agnotocastor*. The latter, however, possesses a  $P^3$ , unlike any other castorid. The skull of *Neatocastor* is not flattened and broad as in palaeocastorines. Wahlert (1977) noted two primitive features of the skull that separated *Agnotocastor* from all other castorids: the stapedia foramen was retained in the bulla and the posterior palatine foramina were entirely within the palatine bone. In all other castorids, the stapedia foramen is lost and the posterior palatine passes through the palatine-maxillary suture more anteriorly than in *Agnotocastor*. The bulla of *Neatocastor* is not preserved but it is evident that the posterior palatine foramen is entirely within the palatine bone as in *Agnotocastor*. The posterior extent of the nasals dorsally on the skull of *Neatocastor* (more posterior than premaxillaries) is unlike any castorines, palaeocastorines, or castoroidines in which the nasals are level with or shorter than the premaxillaries. The incisors of palaeocastorines are anteriorly flattened unlike those of *Neatocastor* and all other castorids. The upper cheek tooth rows are parallel and widely spaced in *Neatocastor* unlike those of other castorids except *Agnotocastor*. The premolars in castorines, castoroidines, and most palaeocastorines are the largest of the cheek teeth. The premolars in *Neatocastor* are subequal in size to the molars in early stages of wear. Because the crowns of the molars taper toward their bases, in latest stages of wear the molars become shorter (anteroposteriorly) than the premolars in *Neatocastor* and all other castorids.

*Neatocastor* differs from species of *Agnotocastor* in being larger with higher-crowned cheek teeth. Cranially, there is little difference between these two genera. Both are characterized by elongate rostra, premolars subequal in size to the molars (not enlarged), and having the maxillary tooth rows parallel rather than divergent. The complexity of the occlusal pattern of the cheek teeth of *Neatocastor* is quite similar to that of *Agnotocastor*: the upper molars retain the elongate J-shaped mesoflexus with multiple fossettes, and the lower cheek teeth preserve the irregularities of the enamel along the borders of the various fossettids even in worn specimens. *Agnotocastor* retains a  $P^3$  (primitive for castorids) whereas in *Neatocastor* a  $dP^3$  is present in juvenile individuals but is not replaced by the permanent tooth.

*Neatocastor hesperus* (Douglass, 1901)  
(Fig. 1, 2; Table 1)

*Steneofiber complexus* Douglass, 1901:249.

*Steneofiber hesperus* Douglass, 1901:243.

*Monosaulax complexus* (Douglass) Stirton, 1935:421.  
*Monosaulax hesperus* (Douglass) Stirton, 1935:422.  
“*Monosaulax*” *complexus* (Douglass) Wilson, 1960:72.  
“*Monosaulax*” *hesperus* (Douglass) Wilson, 1960:72.  
*Steneofiber hesperus* (= *complexus*) Douglass: Xu, 1994:85.

**Type Specimen.**—CM 711, left mandible with complete dentition.

**Referred Specimen.**—CM 712 (holotype of *Steneofiber complexus*), partial skull with incisors, dP<sup>4</sup>–M<sup>3</sup> and unerupted P<sup>4</sup> on the right side, and associated mandibles with incisors and dP<sub>4</sub>–M<sub>3</sub>; right P<sub>4</sub> preserved in crypt.

**Horizon and Locality.**—Holotype from Blacktail Deer Creek, Beaverhead County, Montana. Referred specimen from gray sandy layer that cuts through White River-age rocks on the west side of the Madison River nine or ten miles south of Three Forks, Gallatin County, Montana.

**Age.**—CM 711 is from the Arikareean (late Oligocene) Black Tail Deer Creek fauna (see Hibbard and Keenmon, 1950). CM 712 was described from a horizon of unknown age by Douglass (1901). An age determination was not made by Douglass because of the lack of associated mammal fossils. Later, Wood (1933) described specimens of the Arikareean rhinocerotid *Diceratherium armatum* from the same beds but a different locality, establishing the age as Arikareean. Stirton (1935) mistakenly listed both *S. hesperus* and *S. complexus* as being questionably late Miocene (= Barstovian) in age. The age of both CM 712 and CM 711 is clearly Arikareean as noted by Xu (1994).

**Description.**—The skull of *N. hesperus* (CM 712) is badly damaged and little more than the size and shape of the rostrum is preserved. The rostrum is long (upper diastema 22.7 mm in length), laterally narrow, and not very deep (dorsoventral measurement 11.9 mm) compared to contemporaneous palaeocastorine beavers. The only recognizable foramina on the rostrum are the incisive foramina and the infraorbital foramen on the left side. The incisive foramina are long (3.9 mm) and narrow slits positioned in the center of the anterior part of the palate (diastema). The premaxillary–maxillary suture intersects the center line of the rostrum at the posterior end of the incisive foramina. The infraorbital foramen is low on the rostrum and dorsal to the posterior ends of the incisive foramina. Laterally, the infraorbital foramen is shielded by a flange of bone.

Dorsally, the nasals and premaxillary bones extend posteriorly, level with the anterior margin of the orbits. The nasals extend about 1.8 mm farther posterior than the premaxillaries. A parasagittal crest arises from the posterior margin of the orbit and is directed posteriorly and slightly medially. Only the anterior part of the right parietal is preserved, so it cannot be determined whether there is a sagittal crest at the back of the skull. In *Agnotocaster* there is a single sagittal crest that runs the length of the cranium from a point even with the center of the orbits.

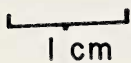
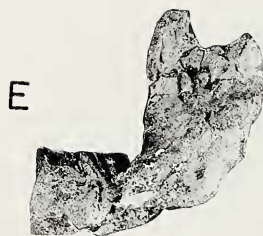
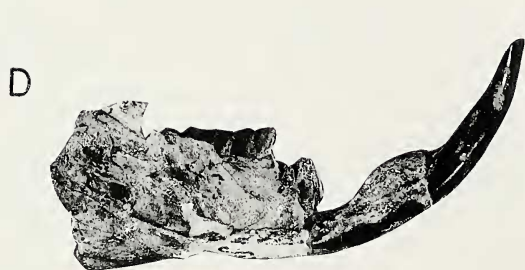
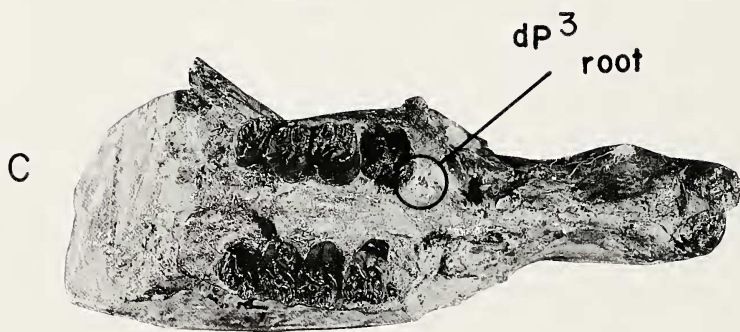
The zygomatic plate is broken away on both sides of the skull and the medial orbital wall is badly crushed, eliminating any evidence of foramina or sutures. However, most of the anterior portion of the palate is preserved. The palatine–maxillary suture extends anteriorly to the level of the anterior margin of the first molars. The posterior palatine foramina are even with the center of M<sup>1</sup> within the palatine bone. The palatal surface is smooth with no indication of any grooves or furrows.

The tooth rows are parallel. The ventral surface of the upper diastema is nearly flat with only a slight dorsal inclination.

The upper incisors are broad with gently convex enamel faces. They appear somewhat procumbant, similar to the condition in *Palaeocaster* (Stirton, 1935:fig. 31). The cheek teeth are subhypsodont. P<sup>4</sup> and the first two molars are subequal in size, M<sup>3</sup> is slightly smaller. On the right side of the skull there is a small peg anterior to the tooth row which appears to be the root of dP<sup>3</sup>. In a maxillary specimen listed by Rasmussen (1977) as “*Monosaulax*” *complexus* there is no P<sup>3</sup> associated with the adult dentition, and since dP<sup>4</sup> is still present in CM 712, it is most likely that the root belongs to a deciduous premolar rather than a permanent P<sup>3</sup>. DP<sup>4</sup> is lower crowned and slightly smaller than the molars; its occlusal pattern is complex and reminiscent of the molars. There is a long paraflexus that extends lingually, and the sides of the paraflexus are irregular, not straight. A shallow hypoflexus extends from the lingual margin of the tooth anterobuccally and nearly meets the lingual end of the paraflexus. The anterior arm of the hypocone and posterior arm of the protocone fuse near the center of the tooth and extend to the buccal margin of the tooth as a thin loph (= ?mesoloph) which bisects the occlusal surface of the tooth. Anterior to the buccal end of this loph is a minute, circular fossette between the ?mesoloph and the paraflexus. Posterior to the ?mesoloph are three separate fossettes. The largest one is crescentic and forms most of the posterior border of the ?mesoloph. A smaller, ovate fossette is on the posterobuccal corner of the tooth. The last fossette is minute and is near the center line of the tooth along the posterior margin.

P<sup>4</sup> is preserved in CM 712 on the left side but still remains in the crypt. The surface consists of a







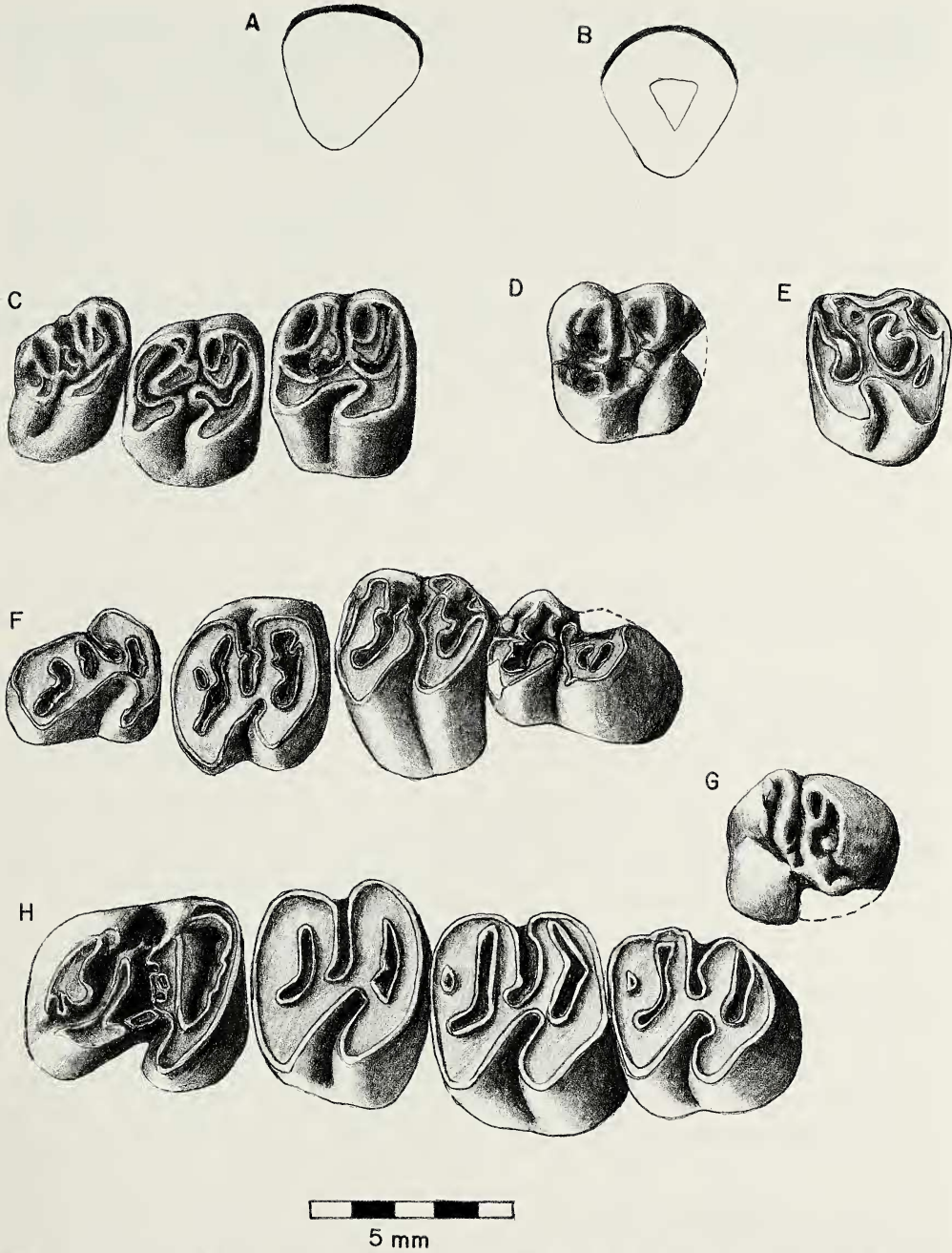


Fig. 2.—Dentitions of *Neotocastor hesperus*. A, C–G, CM 712. B, H, CM 711 (holotype). A, cross section of right I<sub>1</sub>. B, cross section of left I<sub>1</sub>. C, right M<sup>1</sup>–M<sup>3</sup>. D, right P<sup>4</sup> (in crypt). E, left dP<sup>4</sup>. F, left dP<sub>4</sub>–M<sub>3</sub>. G, partial right P<sub>4</sub> (in crypt). H, left P<sub>4</sub>–M<sub>3</sub>.

←  
Fig. 1.—Skull and mandible of *Neotocastor hesperus*, CM 712 (holotype of “*Steneofiber complexus*”). A, right lateral view of skull. B, ventral view of skull. C, dorsal view of skull. D, lateral view of left mandible. E, lateral view of right mandible.

series of lophs that are covered with enamel that is crenulated and irregular. As in  $dP^4$  there is a deep parafofsette and shallow hypofossette that nearly meet. There is a central mesoflexus that extends lingually for nearly the entire width of the tooth. Between the mesoflexus and paraflexus is a smaller, ovate fossette along the buccal margin of the tooth. Posteriorly there is a wide (buccolingually) metafofsette that runs the entire width of the tooth. The metafofsette opens posteriorly through a shallow valley that may close in early stages of wear. All of the lophs that separate the flexi and fossettes of  $P^4$  are covered with irregular enamel that may produce any number of minute fossettes once the tooth is in occlusion and the lophs begin to wear.

$M^1$  and  $M^2$  are equal in size. As in  $P^4$  the flexi and fossettes have irregular walls reflecting the enamel irregularities along these lophs. On  $M^1$ , there is a long parafofsette that may have opened buccally when unworn. The parafofsette curves posteriorly at its lingual end, forming a "J" in shape. Similarly, the mesoflexus curves posteriorly at its lingual end, extending posteriorly to the posterior margin of the tooth. The hypoflexus is shallow and directed anterobuccally. Two other small fossettes are present along the buccal edge of the tooth. The first is the smallest and is situated between the paracone and the mesoflexus. The posterior one (metafofsette) is larger and located in the postero-buccal corner of the tooth posterior to the metacone. The hypostria extends nearly to the base of the tooth on the lingual side. The mesostria is short, extending less than half the buccal height of the crown. All of the upper molars taper dorsally. In late wear this tapering is manifest in the anteroposterior shortening of the molars.

$M^2$  is nearly identical to  $M^1$  except in a few features which may be due to a lesser amount of wear. On  $M^2$  the hypoflexus is continuous with the paraflexus on the left side but not on the right. Also on the right, the mesoflexus is continuous with the metafofsette at the lingual end. On the left side a posteriorly directed portion of the mesoflexus is closed anterior to the metafofsette. A distinct mesocone is present on both  $M^2$ s.

$M^3$  is the smallest of the cheek teeth and is in a very early stage of wear. The paraflexus and hypoflexus are confluent and the paraflexus has a shallow anterior opening at its buccal end. A distinct mesocone is present. There are four buccolingually elongate fossettes along the buccal margin of the tooth.

The mandible is dorsoventrally deep, as is typical of castorids. The masseteric fossa ends anteriorly below the anterior margin of  $M_1$ . The diastema is shallow, concave dorsally, and nearly as long as the length of the tooth row. The mental foramen, preserved only on CM 711, is at middepth of the mandible just anterior to the anterior margin of  $P_4$ . The ascending ramus rises steeply dorsally, beginning at the level of  $M_2$ , and a broad, shallow valley separates the tooth row from the medial border of the ascending ramus. The coronoid process is short and extends vertically, well dorsal to the occlusal surface of the cheek teeth. The articular condyle is directly posterior to the coronoid and just slightly ventral to it. The angle of the mandible is medially deflected, not in line with the ascending ramus.

The lower incisor, like the upper incisor, is broad and gently convex anteriorly. As in the upper cheek teeth, the lophs of the lower cheek teeth are covered with enamel that has numerous irregularities. The  $dP_4$  is smaller than the molars and much lower crowned. In occlusal shape, it is narrow anteriorly and wider posteriorly. The hypoflexid is short and posteriorly directed. There is a small buccolingually elongated fossettid along the posterior edge of the tooth. The mesofossettid is split into two by a short loph (= ?mesolophid). On the right side, this fossettid is completely divided into two separate fossettids, whereas on the left side these two smaller fossettids are still joined at their lingual ends. Anteriorly, there is a crescentic parafofsettid.

The lower permanent premolar is preserved not only in the holotype (CM 711) but also in the crypt below  $dP_4$  on the right side of CM 712. The premolar is subequal in size to the anterior molars. Anteriorly there is a long parafofsettid that extends the entire width of the tooth. It curves anteriorly at its buccal end and opens anteriorly through a shallow valley in the anterior wall of the tooth. The posterolingual end of the parafofsettid appears to close off from the remainder of the fossettid in late stages of wear, isolating an additional fossettid. The mesoflexid is very shallow, and a small triangular fossettid (mesofossettid) is isolated near the center of the tooth. The hypoflexid is also shallow and split buccally by a distinct mesoconid. The metafofsettid is buccolingually elongated and runs nearly the entire width of the tooth. Between the metafofsettid and the mesofossettid are numerous minute fossettids that may disappear in later wear. Both the mesostriid and hypostriid extend to the base of the crown.

The unworn molars of CM 712 preserve more complexity of the occlusal surface than do the more worn teeth of the holotype. The first two molars of the holotype consist of a deep mesoflexid and hypoflexid that extend at least to the centerline of the tooth, and two transversely elongate fossettids, parafofsettid and metafofsettid. Both the parafofsettid and mesoflexid curve anteriorly at their buccal ends. Irregularities along the edges of the fossettids are remnants of the kind of enamel irregularities seen on the more unworn molars. The hypostriid extends to the base of the crown, whereas the



mesostriid is very shallow on the lingual side and would be eliminated after only moderate wear. The last molar of the holotype is similar to the anterior molars but is smaller and slightly reduced posteriorly. The less worn molars of CM 712 have the same basic pattern as those of the holotype but retain numerous minute lophules and reentrants in the fossettids.

*Discussion.*—Stirton (1935) referred both *Steneofiber complexus* and *S. hesperus* to the generally Barstovian-aged genus *Monosaulax*. Wilson (1960) noted that this was an incorrect allocation that was based only on the shape of the incisors but he did not allocate these species to any other genus, citing them only as “*Monosaulax*.” Xu (1994) listed *S. complexus* as a junior synonym of *S. hesperus* with no discussion of the comparative morphology of their respective type specimens. It does appear, however, that these two species are synonyms. The holotype of *S. complexus* is a young individual that retains the deciduous dentition. However, both the right permanent upper and lower premolars are preserved in their crypts, which allows for direct comparison with the holotype of *N. hesperus* (CM 711). The lower premolars are essentially identical on CM 712 and CM 711, differing only in the greater complexity of the unerupted tooth in CM 712. Similarly, the lower molars of CM 712 are more complex than those of CM 711, in which the reduction in complexity is clearly due to its more advanced stage of wear.

Douglass (1901), in describing both these species, cited four differences: 1) the lower incisor of *S. complexus* was less convex than that of *S. hesperus*, 2) the angle of the mandible was broadly rounded in *S. complexus* and acute in *S. hesperus*, 3) the buccal cusps of the lower cheek teeth were rounded externally in *S. complexus* and angular in *S. hesperus*, and 4) the lingual border of the lower cheek teeth of *S. complexus* was concave (not straight). These features do not appear to be consistent with the holotypes of these species. The anterior surface of the lower incisor is nearly identical in CM 711 and CM 712. The angle of the mandible in both specimens is broken, so the complete shape is not discernible. As for the shape of the lower cheek teeth, the differences cited by Douglass (1901) are clearly due to the greater degree of wear on CM 711. In crown height and complexity of the occlusal surface of the cheek teeth, and cross-sectional shape of the lower incisor, *S. complexus* is identical to *S. hesperus*. In size, the lower cheek teeth of the holotype of *N. hesperus* are only slightly larger than CM 712 (Table 1).

The greatest difference between *N. hesperus* and species referred to *Monosaulax* is the lack of complexity of the lophs of the cheek teeth and the relatively enlarged premolars of the latter. The lophs separating the fossettes (-ids) or flexi on the cheek teeth of *Monosaulax* species are simple, smooth, and generally straight. The lophs of the cheek teeth of *N. complexus* are complicated with minute ridges and crenulations. The premolars of *Monosaulax* are larger than any of the molars, whereas in *Neotocastor* the premolars are approximately equal in size to at least the first molars in early stages of wear.

Xu (1994) included the European species *Steneofiber jaegeri* and *S. depereti*, as well as two Asian species, *Monosaulax changpeinensis* and *M. tungurensis*, as synonyms of *S. hesperus*. He cited three features that united these species and separated them from *Eucastor* (which he cited as a senior synonym of *Monosaulax*): 1) jugal contacts the lacrimal bone and straight masseter ridge (masseteric fossa adjacent to the infraorbital foramen); 2) condyle, coronoid process, and angle of the mandible form straight line in posterior view (not aligned as in *Eucastor*); and 3) *Eucastor* has a cheek tooth pattern with fewer flexi.



Table 1.—Dental measurements of *Neotocastor hesperus*. Abbreviations: a-p, anteroposterior length; tr, maximum transverse width; \* indicates estimated dimensions of permanent premolars in crypt.

			CM 712	
		CM 711	Right	Left
I <sub>1</sub>	a-p	3.68	3.62	3.49
	tr	3.71	3.50	3.41
dP <sub>4</sub>	a-p		4.28	3.50
	tr		2.99	3.12
P <sub>4</sub>	a-p	5.10	4.50*	
	tr	4.40	3.30*	
M <sub>1</sub>	a-p	3.80	3.22	3.47
	tr	4.30	4.15	3.94
M <sub>2</sub>	a-p	4.00	3.54	3.49
	tr	4.05	3.82	4.04
M <sub>3</sub>	a-p	3.80	3.21	2.96
	tr	3.60	3.30	2.96
I <sup>1</sup>	a-p		3.22	3.40
	tr		3.69	3.71
dP <sup>4</sup>	a-p			3.40
	tr			3.85
P <sup>4</sup>	a-p		3.80*	
	tr		3.80*	
M <sup>1</sup>	a-p		3.40	3.20
	tr		4.10	4.00
M <sup>2</sup>	a-p		3.00	2.95
	tr		4.00	3.90
M <sup>3</sup>	a-p		2.30	2.50
	tr		3.50	3.65

The use of these characters is not consistent with the record of “*Steneofiber hesperus*.” The only known skull of *N. hesperus* is CM 712, and it is damaged in such a way that these particular cranial features are not preserved at all. Similarly, of the three lower jaws of the American beaver, none has all three processes of the mandible preserved (condyle, coronoid, angle), so their alignment is impossible to determine. The right mandible of CM 712 preserves a part of the angle and it is more medial than the remainder of the ascending ramus, at least hinting that the posterior mandibular processes are unlike those of *Steneofiber*. The skull of *N. hesperus* also preserves the root of dP<sup>3</sup> on the right side. In *Steneofiber*, as in all other castorids except *Agnotocastor*, this tooth is lost. As for the number of flexi on the cheek teeth, Xu (1994) may be correct in number, but his discussion and figures do not detail the great amount of complexity in the pattern of *N. hesperus* teeth. The cheek teeth of *Steneofiber*, as well as *Monosaulax* and *Eucastor*, are a series of reentrant valleys separated by smooth, straight lophs. The lophs of the cheek teeth of *Neotocastor* are far more complicated with numerous lophules and tuberosities that are preserved even in worn teeth.

Some cranial features that Xu (1994) did not consider also preclude *Neotocastor* from being a species of *Steneofiber*. The most obvious feature of the skull of *N. hesperus* is the elongation of the rostrum, which it shares with *Agnotocastor*. In the type of *N. hesperus* the upper diastema is 175% the length of the upper tooth row. In *Agnotocastor praetereadens* this ratio is 150%. In the skulls of *Steneofiber* figured by Stirton (1935:fig. 14–18) the ratio of the diastemal length to the tooth row ranges from 100 to 125%. The incisive foramen is also relatively larger in

*Neotocastor* and *Agnotocastor*. The ratio of the length of the incisive foramen to the length of the upper diastema in *Agnotocastor* and *Neotocastor* is 0.39 and 0.33, respectively. In the figured skulls of *Steneofiber* this ratio is 0.23–0.25, much shorter. The more posterior extent of the nasals on the dorsal skull of *Neotocastor* is not present in skulls of *Steneofiber* where the premaxillary and nasal bones extend posteriorly to the same level as in other castorids.

Wahlert (1977) separated *Agnotocastor* from all other castorids based on two primitive characters: presence of a stapelial foramen on the bulla (lost in other castorids), and posterior palatine foramina entirely within the palatine bone (along palatine–maxillary suture in other castorids). In a skull of *S. castorinus* (AMNH 11010) are two pairs of posterior palatine foramina, a large pair along the palatine–maxillary suture (typical of castorines), and a minute pair posterior to them in the palatine bone. The skull of *N. hesperus* preserves only the anterior portion of the palatine bone on the palate and the entire palatine–maxillary suture is distinguishable. The posterior palatine foramina are posterior to the suture, the condition in *Agnotocastor* and unlike *Steneofiber* and all other castorines. Clearly, *N. hesperus* is not a species of *Steneofiber*.

The European species that Xu (1994) listed as synonyms of “*Steneofiber*” *hesperus* cannot be referred to *Neotocastor*. Not only do the cheek teeth of these species lack the complexity of *N. hesperus*, but they are markedly larger. Wilson (1960) noted that a species he referred to *Anchitheriomys* from the Hemingfordian of Colorado was similar in size to both *Steneofiber depereti* and *S. jaegeri*. This Colorado species is 30% larger than *N. hesperus* (Wilson, 1960:67). Stehlin and Schaub (1951:fig. 80) figured an upper molar of *S. jaegeri* that is nearly 40% larger than the upper molars of *N. hesperus*. Stirton (1935:415) listed dental measurements of “*Steneofiber*” *depereti* that are nearly twice as large as the dental measurements of *N. hesperus* (Table 1). Also, no species of *Steneofiber* is known to have a  $dP_3$  as in *Neotocastor*. These European species clearly are not synonyms of *N. hesperus* and should be retained in *Steneofiber* as originally designated.

The Asian species listed as synonyms of “*S.*” *hesperus* by Xu (1994), likewise, cannot be referred to this species. The early Miocene *Monosaulax changpeiensis* differs from the Montana species in a number of dental features. The  $P_4$  of *M. changpeiensis* is characterized by a deep mesoflexid that bends anteriorly, fusing with a parafoesettid that is closed anteriorly (Li, 1962:fig. 1). In a worn  $P_4$  the flexid is closed lingually but the foesettid maintains its long and curved shape. The  $P_4$  of *N. hesperus* has an open anterior flexid, and there is a loph that separates the mesoflexid from the parafoesettid. Another feature that separates the  $P_4$  of *M. changpeiensis* from *N. complexus* is the morphology of the metafoesettid. In the unworn specimen of *M. changpeiensis* are two small foesettids, and in the worn specimen is a single, small foesettid that is obliquely oriented. The  $P_4$  of *N. hesperus* has only a single metafoesettid that is long and buccolingually oriented. The lophs of the cheek teeth of *N. hesperus* preserve a number of minor irregularities not present in the teeth of *M. changpeiensis*. The mesostriids on the molars of *M. changpeiensis* also appear to extend lower on the crowns than those of *N. hesperus* (Li, 1962:pl. 1, fig. 1c).

The later Miocene *Monosaulax tungurensis* is known from a mandible that retains  $dP_4$  along with the molars as does the type of “*S.*” *complexus* (CM 712). The molars of *M. tungurensis* have lophs that are simpler (lack irregularities) than the molars of *N. hesperus*. The  $dP_4$  of *M. tungurensis* consists of two simple foesettids (para- and metafoesettid) and a simple mesoflexid and hypoflexid (Li,

1963:pl. 1). The  $dP_4$ s of *N. hesperus* (CM 712) are worn to the same level as that of the holotype of *M. tungurensis* but are far more complex. The parafofossettid is elongated and bent at a right angle near its center. The mesoflexid is divided into two by what appears to be a mesolophid. The metafofossettid is similar to that of the  $dP_4$  of *M. tungurensis* in shape and orientation, but preserves irregular sides, reflecting the generally more complex nature of the lophs of the tooth. There is a steep wall that extends to about the middle of the mandible anterior to  $P_4$  in *M. tungurensis*. The diastema of the mandibles of *N. hesperus* are shallow and gently convex upward. Clearly, these Asian species cannot be referred to *N. hesperus* as suggested by Xu (1994).

Scott (1893) named *Steneofiber montanus* from the Arikareean of Montana based on a maxilla, some lower cheek teeth, and some associated postcranial bones (YPM-PU 10456). Matthew (1902) figured the teeth of *S. montanus* and noted that it had more complex teeth than *Palaeocastor* (= *Steneofiber*) *nebrascensis* and was similar in size to *S. hesperus*. He did not synonymize *S. hesperus* and *S. montanus* because they represented individuals of very different ages (*S. hesperus* young, *S. montanus* old) but noted their great similarity. Later, Stirton (1935) included Scott's species as ?*Agnotocastor montanus*, but cited the holotype as being lost. Both Stirton and Matthew recognized the complexity of the occlusal pattern of the cheek teeth of *S. montanus*, a characteristic of *Neotocastor hesperus*. It is possible that *S. montanus* and *N. hesperus* are synonyms. The holotype of the former (YPM-PU 10456) does exist but the dental elements of the specimen have been lost, so no direct comparison can be made. In the future, if a larger sample of *N. hesperus* or *S. montanus* is discovered, and individuals of the same age as the holotype of the other species are available, then this comparison can be made. If these species do prove synonymous, then the species would have to be referred to *Neotocastor montanus* (Scott).

#### SYSTEMATIC POSITION OF *NEATOCASTOR*

The most recent classification of the Castoridae listed three subfamilies: Castorinae, Palaeocastorinae, and Castoroidinae (Korth, 1994). The genus *Agnotocastor* was excluded from any of these subfamilies because of its possession of primitive characters of the skull and dentition. Wahlert (1977) noted that the skull of *Agnotocastor* was more primitive than all other castorids. Wahlert cited no derived characters of *Agnotocastor* and left it as a sister group to all other castorids (Wahlert, 1977:fig. 3). Dentally, *Agnotocastor* retains a  $P^3$  which is lost in all other castorids, another primitive retention of the genus (Stirton, 1935). The characters that unite *Agnotocastor* and *Neotocastor*, along with the primitive features of the skull (position of the posterior palatine foramina, at least  $dP^3$  retained), are the elongation of the rostrum, larger incisive foramina, more posterior extent of the nasals, and the greater complexity of the occlusal surface of the cheek teeth. These specializations, as well as the primitively retained characters of the skull cited by Wahlert (1977), are also shared with the problematical genus *Amblycastor* and the Eutypomyidae.

The Eutypomyidae have brachydont to submesodont cheek teeth (lower-crowned than either *Agnotocastor* or *Neotocastor*) with complex occlusal patterns, the last premolars subequal in size to the molars, the upper tooth rows parallel, and  $P^3$  or  $dP^3$  retained; these dental features are shared by *Agnotocastor* and *Neotocastor*. Eutypomyids have elongate rostra, nasals that extend more posteri-



only than the premaxillaries dorsally, and retain the stapedial foramen in the bulla (only definitely known in *Agnotocastor* among the former genera) and the posterior palatine foramen is entirely within the palatine bone, features shared by *Agnotocastor* and *Neotocastor*. The only feature used by Wahlert (1977) to separate the Eutypomyidae from the Castoridae was the occlusal pattern of the cheek teeth. The cheek teeth of *Agnotocastor* and *Neotocastor*, while not being as complex as that of *Eutypomys*, are more complex than other castorids. Both *Agnotocastor* and *Neotocastor* have higher-crowned cheek teeth than eutypomyids, and the crowns of the molars taper towards their roots, typical of all castorids. In later stages of wear, because of this tapering of the crowns, the molars are reduced in length (anteroposteriorly) making the premolars appear larger. This "narrowing" of the molars is not present in *Eutypomys*.

The problematical Hemingfordian and Barstovian genus *Amblycastor* (possibly synonymous with *Anchitheriomys*) also shares the elongated rostrum, posterior extension of the nasals, and complex occlusal patterns of the cheek teeth with *Agnotocastor*, *Neotocastor*, and eutypomyids (Wilson, 1960; Voorhies, 1990). Korth (1994) referred *Amblycastor* and *Anchitheriomys* to the Eutypomyidae based on these characters, whereas previously these latter two genera had been considered castorids (Stirton, 1935; Simpson, 1945). *Amblycastor* has cheek teeth that are at least as high-crowned as those of *Neotocastor*. Voorhies (1990) demonstrated that there was evidence for the presence of a dP<sup>3</sup> *Anchitheriomys* (= *Amblycastor*) *fluminis*. A nearly complete skull of this latter species from the Barstovian of Nebraska (USNM 298914, not yet described fully) has the posterior palatine foramina on this specimen entirely within the palatine bone as in *Agnotocastor*, *Neotocastor*, and eutypomyids. The cheek teeth of *Amblycastor* and *Anchitheriomys* have several castorid characteristics not present in eutypomyids: 1) premolars are the largest of the cheek teeth; 2) crowns of the molars taper toward their bases (also present in *Agnotocastor* and *Neotocastor*); and 3) the tooth rows diverge posteriorly, although not as strongly as in other castorids (for descriptions of the skull and dentition of *Amblycastor* and *Anchitheriomys* see Stirton, 1935; Wilson, 1960; Voorhies, 1990). The incisors of *Amblycastor* have been described as procumbent (extending anterior to the premaxillaries), similar to those of *Neotocastor* and *Agnotocastor* (Wood, 1937:pl XXVIII, fig. 1), and distinct from those of castorines such as *Steneofiber* and *Castor* (Stirton, 1935: fig. 15, 16; Voorhies, 1990).

*Agnotocastor*, *Neotocastor*, and *Amblycastor* retain a primitive cranial feature lost in all other castorids: posterior palatine foramina entirely within palatine bone. Other features of the skull shared by these genera are the relative elongation of the rostrum, the nasals extending farther posterior than the premaxillaries dorsally, and procumbent incisors. These features, along with the complexity of the cheek teeth, unite these three genera. Within this group of genera, *Neotocastor* is clearly intermediate in dental characters. The cheek teeth are higher crowned than in *Agnotocastor* and lower crowned than in *Amblycastor* (and *Anchitheriomys*), and the degree of complexity of the occlusal surface of the cheek teeth of *Neotocastor* is less than in *Agnotocastor* and more complex than in *Amblycastor*. However, the Asian species of *Anchitheriomys* have occlusal patterns of the cheek teeth as complex as those of eutypomyids.

If elongation of the rostrum and complex occlusal pattern of the cheek teeth are considered derived characters, then *Agnotocastor*, *Neotocastor*, and *Amblycastor* represent a distinct clade among castoroids closely related to the Eutypo-

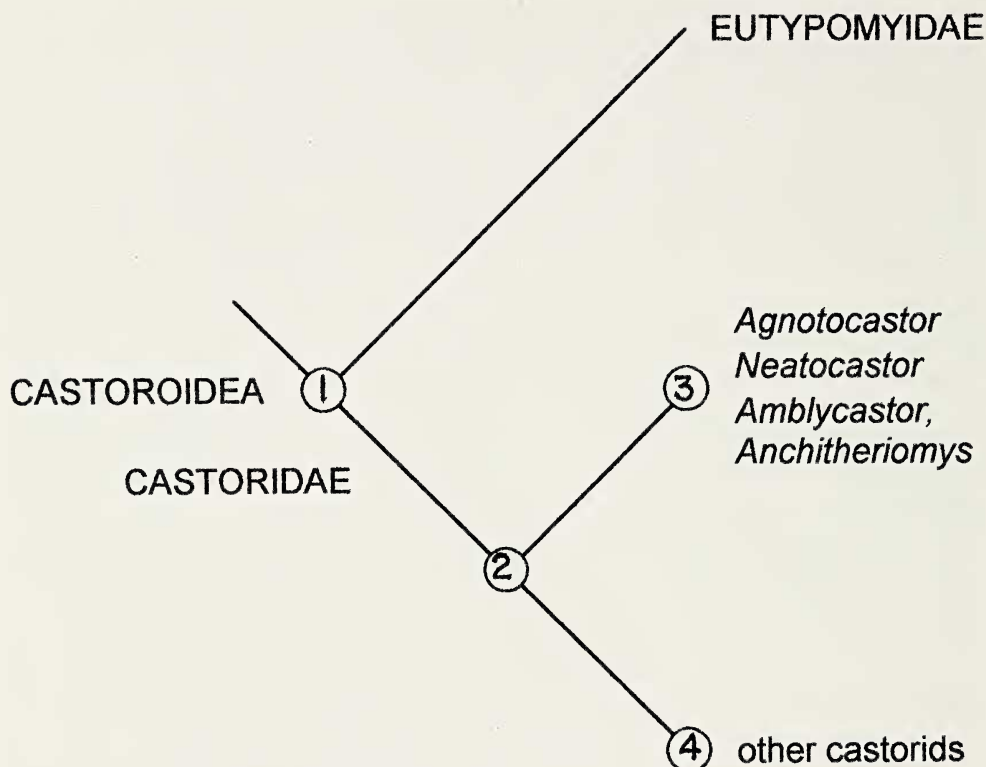


Fig. 3.—Cladogram of proposed relationships. Explanation of nodes: 1, Castoroidea: sciuromorphy; uniserial enamel of incisors; interorbital foramen posterior to optic foramen; sphenopalatine foramen surrounded by maxillary; posterior maxillary foramen enclosed; dorsal palatine foramen in maxillary or along orbitosphenoid-maxillary suture (see Wahlert, 1977:fig. 3). 2, Castoridae: intermediate to large-size rodents; cheek teeth at least mesodont; castorid crown pattern of cheek teeth (= crowns of molars taper towards base; occlusal patterns of cheek teeth series of lophs and reentrant valleys [cusps indistinguishable], patterns become simpler with wear). 3, (unnamed taxon): elongate rostrum; occlusal pattern of cheek teeth complex; upper incisors procumbent; nasals extend further posteriorly than maxillaries dorsally. 4, Palaeocastorinae, Castorinae, Castoroidinae:  $P^3$  and  $dP^3$  lost; stapedial foramen lost; posterior palatine foramen within palatine-maxillary suture; upper tooth rows strongly diverge posteriorly; premolars larger than molars.

myidae. However, if these features are considered primitive for the Castoroidea or convergent with eutypomyids, then these genera represent a primitive group of castorids. The characteristic tapering of the molars that results in a narrowing with age is clearly a dental character that is shared by *Agnotocastor*, *Neotocastor*, *Amblycastor*, and all other castorids.

*Agnotocastor*, *Neotocastor*, and *Anchitheriomys* represent a distinct subfamily of beavers. A name is being proposed formally elsewhere along with a complete description of the skull of *Anchitheriomys* (Korth and Emry, in press). The relationships of this group of genera are presented in Fig. 3.

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